

A New Model Accounting for Seasonal Cessation of Growth in Fishes

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Abstract

A modified version of the von Bertalanffy growth function (VBGF) is proposed in which a sine wave modifies a standard version of the VBGF, enabling a smooth transition between rapid summer growth and a variable period of zero growth (in length) during winter or during the dry season for aestivating fishes. The key features of a nonlinear routine for fitting this new model are also presented, with emphasis on the estimation of the period of zero growth. Application examples, to *Salmo salar* and *Trisopterus esmarkii*, are presented.

Introduction

It is well established that, in temperate waters, the growth of finfishes and aquatic invertebrates (henceforward, 'fishes') displays strong seasonal oscillations mainly due to fluctuations of temperature and/or food supply (Shul'man 1974). Although ubiquitous and detectable when appropriate methods are used, the seasonal growth oscillations of tropical fishes are generally less pronounced (Longhurst and Pauly 1987). However, strong seasonal growth oscillations do exist in the tropics, e.g. where the seasonal contraction of floodplains forces fishes either into small residual ponds, as in the case of bichir (Daget and Ecoutin 1976), or into subterranean aestivation, as in the case of lungfishes (Nikolsky 1963), or where the seasonal temperature differences are pronounced, as in the inner Persian Gulf (Morgan 1985). Thus, one may experience cases, even in the tropics, in which long periods with zero growth in length occur (Fig. 1), along with substantial loss of weight. We shall refer to such periods as no-growth time (NGT). Seasonally oscillating versions of the von Bertalanffy growth function (VBGF), which simply combine the standard VBGF with a sine wave, can not well describe situations in which NGT occurs.

One seasonally oscillating version of the VBGF, developed by Hoenig and Choudary Hanumara (1982) and independently by Somers (1988) (see Hoenig and Choudary Hanumara 1990), takes the form

$$L_t = L_\infty \{1 - \exp - [K(t - t_0) + S \sin 2\pi(t - t_2) - S \sin 2\pi(t_0 - t_2)]\}, \quad (1)$$

where L_t is the predicted length at age t ; L_∞ is the asymptotic length, or the mean length the fish of the population would reach if they were to grow indefinitely; K is the curvature parameter, of dimension time^{-1} (year^{-1} in most seasonally oscillating growth curves),

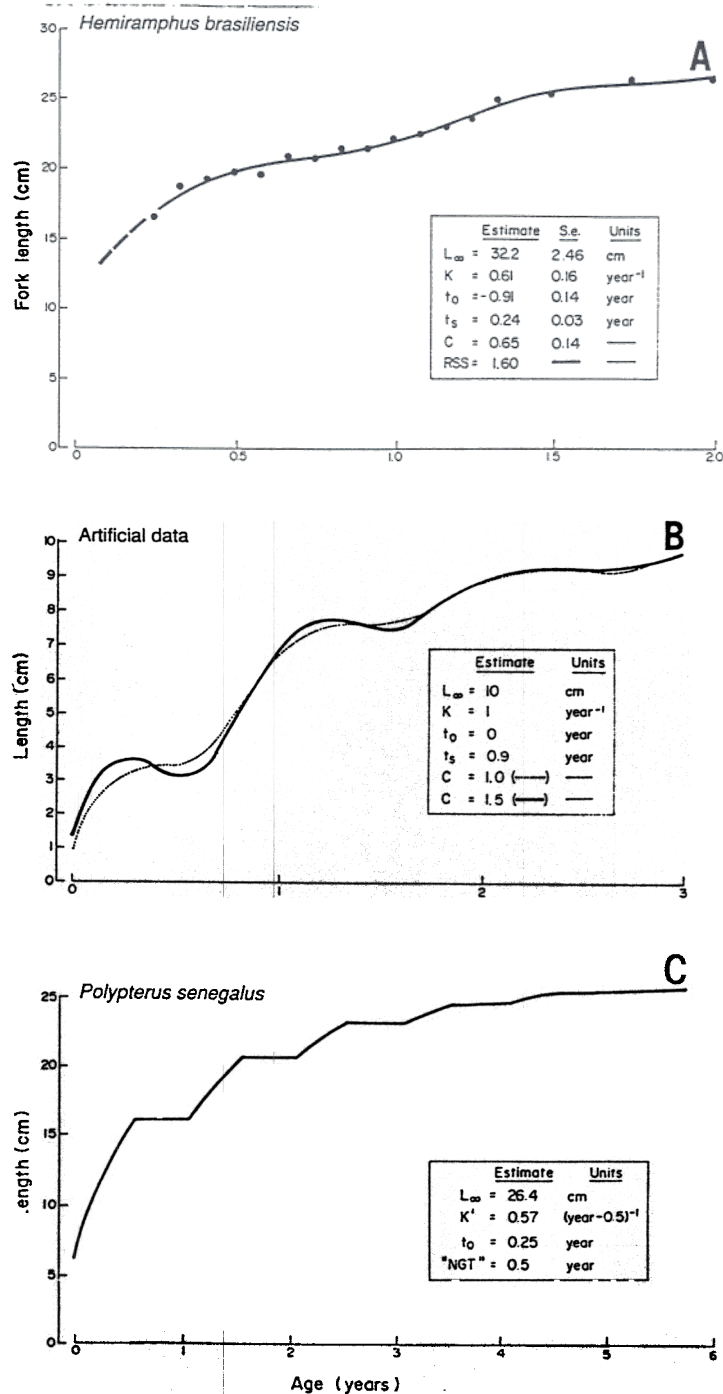


Fig. 1. Seasonally oscillating growth curves, illustrating various aspects of fitting length-at-age data affected by seasonally varying environmental parameters with a suitable growth model. All parameters are defined in the text; standard errors (s.e.) and the residual sum of squares (RSS) are given where available. (A) Plot showing the fit of Eqn 1 to growth data on a subtropical halfbeak (*Hemiramphus brasiliensis*) affected by small variations of temperature, with $C < 1$ (adapted from data in Berkeley and Houde 1978). (B) Plot, based on artificial data, showing that Eqn 1 generates an unrealistic winter shrinkage when $C > 1$; NGT = 0 for $C = 1$. (C) Plot showing the step function resulting from a combination of the standard von Bertalanffy model (Eqn 2) with NGT = 0.5 year in aestivating West African bichir (*Polypterus senegalus*); note the lack of a smooth decline from rapid to zero growth, leading to overestimation of NGT.

expressing the rate at which L_{∞} is approached; t_0 is the theoretical 'age' the fish have at length zero; t_s defines the start of the convex segment of a sinusoid oscillation with respect to $t=0$; and $S=(CK/2\pi)$, where C expresses the relative amplitude of the seasonal oscillation. Thus, the growth rate in length (dl/dt) has exactly one value of zero (at the peak of winter, or of the dry season) when $C=1$, and Eqn 1 reverts to the standard VBGF, or

$$L_t = L_{\infty} \{1 - \exp[-K(t - t_0)]\}, \quad (2)$$

when $C=0$.

Eqn 1 and related models, particularly that of Pauly and Gaschütz (1979), from which Eqn 1 was derived, have been widely used in fish stock assessment (e.g. contributions in Venema *et al.* 1988) and may now be considered standard tools (Pauly 1990). Fig. 1A presents an application example.

However, Eqn 1 and its relatives have a major disadvantage: they can not accommodate periods of no growth. Indeed, when length-at-age data with NGTs are fitted with Eqn 1, the resulting values of C are more than 1, and hence suggest shrinkage (Fig. 1B). This is not realistic for finfish or shellfish whose skeletons largely preclude shrinkage (Ursin 1963, 1979; Nickelson and Larson 1974).

One approach for dealing with this problem, suggested independently by Pitcher and MacDonald (1973) and Daget and Ecoutin (1976), is to 'cut' a growth curve as defined by Eqn 2 into 'growth' and 'no growth' segments; however, this approach is clearly unsatisfactory, relying as it does on an unrealistic step function and hence generating overestimates of NGT (Fig. 1C).

Another approach, proposed by Sager (1984), involves fitting length-at-age data with a model of the form

$$L_t = f(t) - (1 - \epsilon)/(2\pi(1 - k)) * (\delta f(t)/\delta t) * \sin 2\pi \{t - t_a - (k/2\pi) * \sin 2\pi(t - t_a)\} \quad (3)$$

where $f(t)$ is any growth function; ϵ an amplitude parameter, $0 \leq \epsilon \leq 1$; $\epsilon=0$ in the case of growth stagnation; t_a the starting point of an oscillation and k is a parameter related to the duration of the period of reduced growth, $0 \leq k \leq 1$.

This model can fit seasonally oscillating data reasonably well. However, length actually can *decline* during the period of stagnation. Moreover, the duration of this period is not straightforwardly estimated, because it is a function of *both* ϵ and k .

Presentation and Fitting of the New Model

To overcome the abovementioned problems, we devised the equation

$$L_t = L_{\infty} [1 - \exp(-q)], \quad (4)$$

in which

$$q = K(t' - t_0) + K/Q[\sin Q(t' - t_s) - \sin Q(t_0 - t_s)],$$

where $Q=2\pi/(1-NGT)$ and where t' is obtained by subtracting from the real age (t) the total no-growth time occurring up to age t . The symbol for the parameter C has disappeared, but the curve still behaves as if $C=1$, thus enabling smooth transitions between growth and no-growth periods. Seasonal growth itself is described by a sine wave of period $1-NGT$; the unit of K is $(1-NGT)^{-1}$ instead of year^{-1} (in such cases, we shall refer to K' instead of K).

A personal computer program for fitting Eqn 4 to seasonally oscillating length-at-age data has been developed. (This program is available from the first author as an executable MS DOS program; the supplied 360K diskette also contains the data files used to generate Figs 1A, 2 and 3.) The program performs the following operations:

- (1) It stores lengths, ages and weighting factors, if any (e.g. 1/s.e. of mean lengths at age).

(2) It obtains, after a few iterations to identify an appropriate value of L_∞ , an initial set of estimates of K , t_0 , t_s and C from the linearized version of Eqn 1 presented in Soriano and Jarre (1988), i.e.

$$\ln[1 - (L_t/L_\infty)] = -Kt + Kt_0 - (CK/2\pi)\sin 2\pi(t - t_s) + (CK/2\pi)\sin 2\pi(t_0 - t_s), \quad (5)$$

which can be interpreted as multiple linear regression in which

$$\begin{aligned} b_0 &= Kt_0 + (CK/2\pi)\sin 2\pi(t_0 - t_s) \\ b_1 &= -K & X_1 &= t \\ b_2 &= -(CK/2\pi)\cos 2\pi t_s & X_2 &= \sin 2\pi t \\ b_3 &= (CK/2\pi)\sin 2\pi t_s & X_3 &= \cos 2\pi t, \end{aligned}$$

whose value of R^2 is maximized when L_∞ has its appropriate value, and from which

$$\begin{aligned} K &= -b_1 \\ C &= -2\pi b_2 / K \cos(2\pi t_s) = 2\pi b_3 / K \sin(2\pi t_s) \\ t_s &= \tan^{-1}(b_3/b_2) / 2\pi. \end{aligned}$$

The value of t_0 can be obtained only numerically, i.e. by using the Newton-Raphson method of finding the root of the nonlinear equation, viz.

$$t_{0(i+1)} = t_{0(i)} - f(t_{0(i)})/f'(t_{0(i)}),$$

where

$$\begin{aligned} f(t_0) &= Kt_0 + (CK/2\pi)\sin 2\pi(t_0 - t_s) - b_0 \\ f'(t_0) &= K + CK\cos 2\pi(t_0 - t_s), \end{aligned}$$

with an initial guess of $t_0(0) = b_0/K$ (Soriano and Jarre 1988).

(3) (a) If, as a result of operation (2), $C \leq 1$, the program proceeds to nonlinear estimation of L_∞ , K , t_0 , t_s and C and ignores Eqn 4. (b) If $C > 1$, the program proceeds to operation (4).

(4) The program proceeds to nonlinear fitting of Eqn 4, i.e. it estimates L_∞ , K , t_0 , t_s and NGT, using the Gauss-Newton method (Seber and Wild 1989). (a) If NGT = 0, the program goes to operation (3a). (b) If NGT > 0, the program outputs parameter estimates, their standard errors (s.e.), and the residual sum of squares (RSS).

Application Examples and Discussion

Figs 2 and 3 illustrate the application of Eqn 4 to two sets of seasonally oscillating length-at-age data. In the case of Norway pout (Fig. 2), fitting of Eqn 1 instead of our new model would not have caused much of a problem because NGT is short (about 3 weeks). In the case of Atlantic salmon (Fig. 3), the estimated NGT is long (about 3 months), and fitting Eqn 1 instead of Eqn 4 to the data would have led to a value of $C \gg 1$, suggesting shrinkage (as in Fig. 1B).

Silvert (1981) suggested that 'Care should ... be taken to ensure that a simple model is not constructed which artificially distorts valid information. When mathematical forms are fit to scatter plots, it is usually advisable to use functions which act reasonably over their entire range and which capture the major qualitative features of the data. In particular, curves which must pass through the origin should only be fit with curves that pass through the origin; plots that show curvature should not be fit with straight lines; asymmetric data should not be fit with symmetric curves; and curves that do not show specific features should not be fit with curves that exhibit these features without clear justification ...

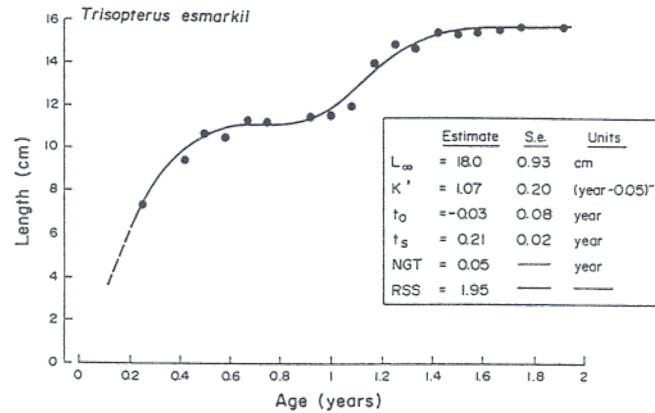


Fig. 2. Seasonally oscillating growth of Norway pout (*Trisopterus esmarkii*) sampled off the Atlantic coast of Scotland (based on data in Gordon 1977). Note the smooth transition to a short NGT of 0.05 year, suggesting that environmental conditions are such that at least a modicum of growth can be sustained throughout most of the year.

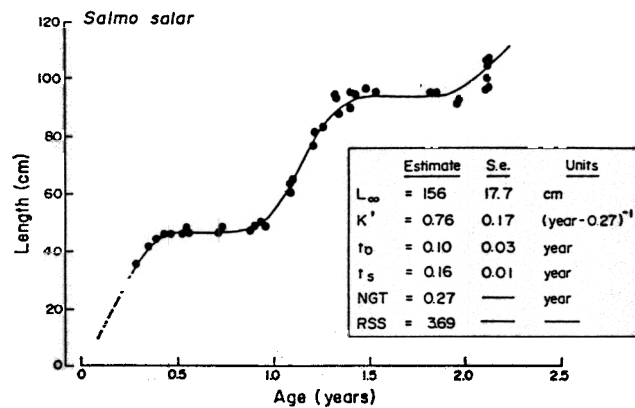


Fig. 3. Seasonally oscillating growth of Atlantic salmon (*Salmo salar*) in the Shelligan Burn, a Scottish stream (based on data in Egglshaw 1970). Note the long NGT of 0.27 year.

It is almost always possible to find a mathematical function with the appropriate qualitative behavior which does not require any more parameters to fit when the most popular model appears inadequate.'

We have presented, with Eqn 4, a model that fulfils several of Silvert's criteria. In particular, this model has no more free parameters than does Eqn 1, which the model complements. In this model, the explicit inclusion of NGT as a variable leads to two sets of benefits: (1) statistically, the residual sum of squares is reduced, and randomly distributed residuals are produced without any additional free parameter having been added; and (2) physiologically and ecologically, the onset, duration and end of NGT can be interpreted relative to the seasonal changes of key environmental factors.

This last point is important in that each set of growth data fitted with Eqn 4 can be interpreted as resulting from a field experiment in which the onset and end of NGT corresponds to the value of a key environmental variable (e.g. availability of food, or temperature) at which growth in length is halted and resumed, respectively.

We shall elaborate elsewhere on this theme, and on the incorporation of Eqn 4 into various stock-assessment models such as length-converted catch curves, length-based virtual population analyses, and yield-per-recruit analyses.

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